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CROSS-TRANSMISSION STUDIES WITH *EIMERIA ARIZONENSIS, E. ARIZONENSIS*-LIKE OOCYSTS AND *EIMERIA LANGEBARTELI*: HOST SPECIFICITY AT THE GENUS AND SPECIES LEVEL WITHIN THE MURIDAE

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ABSTRACT: Cross-transmission experiments were done using sporulated oocysts of *Eimeria arizonensis* from *Peromyscus truei* and *Peromyscus maniculatus,* and oocysts of 2 putative species that resemble *E. arizonensis,* i.e., *Eimeria albigulae* from *Neotoma albigula,* and *Eimeria onychomysis* from *Onychomys leucogaster.* Oocysts of each species were inoculated into representatives of *P. maniculatus* and the latter 2 rodent species. Other experiments were conducted wherein oocysts of *Eimeria langebarteli* from *Peromyscus leucopus* were given to *P. truei* and *P. maniculatus.* Oocysts of *E. arizonensis* from *P. truei* and *P. maniculatus* could be transmitted only to *P. maniculatus*; likewise, oocysts of *E. albigulae* and *E. onychomysis* produced patent infections only in *N. albigula* and *O. leucogaster,* respectively. Oocysts of *E. langebarteli* from *P. leucopus* could be transmitted to *P. truei,* but not *P. maniculatus.* These results indicate that *E. arizonensis,* and the morphologically similar *E. albigulae* and *E. onychomysis,* are distinct species that are not transmissible between the genera of their respective hosts (*Peromyscus, Neotoma, Onychomys*), and that some isolates of *E. langebarteli,* reported from 6 species of *Peromyscus* and *Reithrodontomys megalotis,* may not always be infective to *P. maniculatus.*

Eimeria, with over 1,100 described species (Levine, 1988), is the most speciose of all apicomplexan genera. The case of *Eimeria arizonensis* exemplifies the problems rife in the taxonomy of this, and other, genera of coccidia, e.g., *Isospora, Cryptosporidium.* Contrary to the tenet that the *Eimeria* of rodents are highly host specific, it is 1 of the most ubiquitous parasites of North American murid rodents, having been reported from 8 species of *Peromyscus* and 3 species of *Reithrodontomys* (Duszynski et al., 1992; Upton et al., 1992; McAllister et al., 1993), and it can be passaged between hosts from these genera (Upton et al., 1992). *Eimeria arizonensis* can be difficult to identify because its oocysts may vary in a number of morphological features, depending upon the host from which it is recovered (Duszynski et al., 1992; Upton et al., 1992). Moreover, the sporulated oocysts of 2 other coccidia, *Eimeria albigulae* and *Eimeria onychomysis,* often are indistinguishable from those of *E. arizonensis* (Upton et al., 1992). These *E. arizonensis*-like species have been reported from hosts within the murids *Neotoma* and *Onychomys,* respectively (Levine et al., 1957; Reduker and Duszynski, 1985), rodents known to be sympatric with *Peromyscus* species (Findley et al., 1975; Hoffmeister, 1986). Concerned that these 3 species of *Eimeria* might not be distinct, Upton et al. (1992) performed cross-transmission experiments that suggested that they were host-specific forms. However, they cautioned that the interpretation of their results was limited by the small sample sizes and unknown immune status of each experimental host and that, under natural conditions, successful transfers might occur among syntopic hosts. The present cross-transmission study was conducted to redress these problems by (1) using *Peromyscus* and *Onychomys* subjects that had no previous exposure to coccidia; (2) testing whether *Neotoma* subjects that had been previously exposed to *E. arizonensis* and *E. onychomysis* could support patent infections of *E. albigulae*; and (3) inoculating subjects with isolates of *E. arizonensis, E. albigulae,* and *E. onychomysis* that had been collected from syntopic hosts. In addition, we present data from cross-transmission experiments wherein *Eimeria langebarteli* from *Peromyscus leucopus* was given to *Peromyscus truei* and *Peromysus maniculatus* subjects, and we summarize information on previous attempts to cross-transmit the *Eimeria* of murid rodents from Levine and Iven's (1988) review and subsequent investigations on this topic (Nowell and Higgs, 1989; Ibrahim and Nowell, 1991; Upton et al., 1992).

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MATERIALS AND METHODS

Feces or intestinal contents were collected from wild-caught hosts of 3 genera representing 5 species (Table I) and were processed in 2.5% (w/v) aqueous $K_2Cr_2O_7$ to allow oocyst sporulation as described by Duszynski and Wilber (1997). *Eimeria* spp. were identified using coverslip flotation with a concentrated sucrose solution (specific gravity 1.15) and, depending on the number of oocysts available in a sample, ~20–1,000 oocysts were washed 2–3 times in tap water, resuspended in 0.5 ml tap water and inoculated per os by stomach tube into conspecific or congeneric animals to increase the number of oocysts available for cross-infection trials. The 6 resulting isolates (Table I) and sporulated oocysts derived from them via subsequent infections were stored in 2.5% aqueous $K_2Cr_2O_7$ at ~4 C until used in experimental infections.

All experimental animals were individually housed in plastic cages with presterilized wood shavings and nesting material, given water and commercial rodent food ad libitum, and maintained on 12 hr light/dark cycles in rooms kept at ~23 C. For each of the 3 days prior to an infection trial, samples of each subject's feces were examined to ensure that the animals were not shedding oocysts. For all cross-infection trials, sufficient numbers of the freshest available sporulated oocysts were prepared so that we could concurrently inoculate ~1,000 oocysts into 1 animal of each host species, the normal host serving as a control for that particular trial. Thereafter, all of the feces that could be found from each host were collected daily for 21 days postinoculation (PI) and examined for unsporulated oocysts. The species and isolates of *Eimeria,* the ages of the oocysts inoculated, the recipient host species and number of subjects, the number of trials, and the consequence of each experimental inoculation are given in Table II.

Laboratory-reared *P. maniculatus* (BW stock, subspecies *Peromyscus maniculatus bairdii*) were purchased from the *Peromyscus* Genetic Stock Center, University of South Carolina, and bred to provide F_1 and F_2 generation subjects for cross-transmission experiments. The *P. truei* recipients were collected from The University of New Mexico's Long Term Ecological Research (LTER) site on the Sevilleta National Wildlife Refuge, Socorro Co., New Mexico (see Wilson et al., 1997) and were in captivity for ~2 yr prior to their use in infection trials. *Onychomys leucogaster* were F_1 generation offspring from animals collected at the Sevilleta LTER; adult *Neotoma albigula* experimental subjects also were collected at the Sevilleta LTER and were in captivity ~8 mo

TABLE I. Wild-caught murid rodents from which isolates of 4 *Eimeria* species were derived for use in cross-transmission experiments.

Host	Collection			*Eimeria* spp.	Isolate no.
	ID no.	Locality	Date		
Neotoma albigula	NK40004*	Sevilleta LTER, Socorro Co., New Mexico	October 1995	*E. albigulae*	1
N. albigula	NK40231	Sandia Mountain, Bernalillo Co., New Mexico	September 1995	*E. albigulae*	2
Onychomys leucogaster	NK32792	Sevilleta LTER, Socorro Co., New Mexico	July 1993	*E. onychomysis*	3
Peromyscus truei	—	Sevilleta LTER, Socorro Co., New Mexico	September 1996	*E. arizonensis*	4
P. maniculatus	—	Corvallis, Benton Co., Oregon	April 1995	*E. arizonensis*	5
P. leucopus	NK40473	Sevilleta LTER, Socorro Co., New Mexico	September 1996	*E. langebarteli*	6

* NK = New Mexico karyotype number; specimens deposited in the University of New Mexico Southwestern Museum of Biology.

prior to their use in infection trials. All cross-infections and control infections involving *Onychomys* and *Peromyscus* were performed on subjects that had not had any previous inoculations. Because only 3 captive *N. albigula* were available, all 3 were used for all cross-infection trials, and 1 of the individuals was used for 2 of the 4 control infections with *E. albigulae*. The feces of all captive rodents were checked 1–2 times per mo to ensure that they remained free of coccidia and helminths. During an ~2-yr period, some of the parental and F_1 generation *P. maniculatus* were found to be shedding *Eimeria delicata* (11 mice) or pinworm eggs (*Syphacia* sp., 4 mice); these animals were not used in the cross-infection trials, but all were treated with sulfamethazine (a coccidiostat) or piperazine (an anthelmintic) to eliminate the infections and prevent their spread through the colony. Throughout the study, fecal exams for all other rodents were negative for helminth eggs and coccidia.

RESULTS

The isolates of *E. albigulae* were transmissible to *N. albigula*, the control host, for all 4 trials with this parasite/host combination, but not to *O. leucogaster* or *P. maniculatus* (Table II). Likewise, the isolate of *E. onychomysis* produced patent infections in 4 of 4 trials with the control host *O. leucogaster*, but not in the 4 concurrent trials with *N. albigula* or *P. maniculatus;* similarly, the isolates of *E. arizonensis* were successfully passaged in 4 of 4 trials with *P. maniculatus* (the control host) but not in the 4 concurrent trials with *N. albigula* or *O. leucogaster* (Table II). When the data from this study were combined with the experimental inoculations of *E. arizonensis, E. albigulae,* and *E. onychomysis* into *P. truei, Neotoma mexicana,* and *O. leucogaster* by Upton et al. (1992, see Table III), we find that *E. arizonensis* was successfully passaged through control *Peromyscus* mice (9 of 9 trials) but not *Neotoma* (0 of 5 trials) or *Onychomys* (0 of 6 trials) subjects. Similarly, *E. albigulae* produced patent infections in all 5 trials with control *Neotoma* but not in the cross-infection trials with *Peromyscus* or *Onychomys* (9 and 6 trials, respectively, Table III). *Eimeria onychomysis* was always transmissible to control *Onychomys* (6 trials), but

TABLE II. Experimental protocol and results of cross-infection trials with isolates of 4 species of *Eimeria* inoculated into rodents in the genera *Neotoma, Onychomys,* and *Peromyscus*; all animals received an inoculation dose of ~1,000 oocysts and all were examined daily through 21 days postinoculation.

Eimeria spp.	Isolate no.	Recipients*			Age of oocysts when inoculated (days)	Oocysts present (+), absent (−)
		Species	No. subjects	No. trials		
E. albigulae	1	*N. albigula*†	3	3	435, 133, 97‡	All +, days 6–16§
		O. leucogaster	3	3		All −
		P. maniculatus	3	3		All −
E. albigulae	2	*N. albigula*†	1	1	182	+, days 7–15
		O. leucogaster	1	1		−
		P. maniculatus	1	1		−
E. onychomysis	3	*O. leucogaster*†	4	4	71, 34, 49, 116	All +, days 5–11
		P. maniculatus	4	4		All −
		N. albigula	3	4		All −
E. arizonensis	4	*P. maniculatus*†	3	3	23, 131, 30	All +, days 4–10
		O. leucogaster	3	3		All −
		N. albigula	3	3		All −
E. arizonensis	5	*P. maniculatus*†	1	1	90	+, days 4–11
		O. leucogaster	1	1		−
		N. albigula	1	1		−
E. langebarteli	6	*P. truei*†	3	3	83, 47, 151	All +, days 7–16
		P. maniculatus	3	3		All −

* Same 3 *N. albigula* were recipients for all cross-infections; 1 animal was a recipient for 2 control infections.
† Control hosts.
‡ Ages of inocula are in order of trials in which they were used, i.e., trial 1, trial 2, etc.
§ Patent periods are the ranges observed in this study.

TABLE III. Combined results of this study and Upton et al. (1992) for patent infections observed in cross-infection experiments with isolates of 3 species of *Eimeria* inoculated into rodents in the genera *Neotoma, Onychomys,* and *Peromyscus.*

Host	*Eimeria* species inoculated*		
	E. arizonensis	*E. albigulae*	*E. onychomysis*
P. maniculatus (this study)	4/4†	0/4	0/4
P. truei (Upton et al.)	5/5†	0/1	0/2
Total	9/9†	0/5	0/6
N. albigula (this study)	0/4	4/4†	0/4
N. mexicana (Upton et al.)	0/1	1/1†	0/1
Total	0/5	5/5†	0/5
O. leucogaster (this study)	0/4	0/4	4/4†
O. leucogaster (Upton et al.)	0/2	0/2	2/2†
Total	0/6	0/6	6/6†

* No. of patent infections observed/no. of infection trials.
† Control hosts.

never to hosts in the genera *Peromyscus* or *Neotoma* (9 and 5 trials, respectively, Table III).

The *E. langebarteli* isolated from *P. leucopus* produced patent infections in 3 of 3 trials with *P. truei* (control host) but not in the 3 concurrent trials with *P. maniculatus* (Table II). Prior to these experiments, we were unable to passage sporulated oocysts from the original field sample (Table I) through 3 other coccidia-free *P. maniculatus.* These initial failures led to the inoculation experiments using captive *P. truei* as control hosts, because we had no *P. leucopus* in captivity, and Reduker et al. (1985) had reported successful experimental infections of *E. langebarteli* in *P. truei.*

DISCUSSION

The results of our cross-infection experiments with *E. arizonensis* and the *E. arizonensis*-like oocysts of *E. albigulae* and *E. onychomysis* are consistent with and extend those of Upton et al. (1992) and demonstrate that, although their oocysts are morphologically similar, each is a valid species, with the host ranges of *E. albigulae* and *E. onychomysis* restricted to *Neotoma* and *Onychomys,* respectively, and the host range of *E. arizonensis* including *Peromyscus* and *Reithrodontomys,* but not rodents from the other 2 genera. Upton et al. (1992) were more tentative in suggesting that these are 3 distinct species because they had a limited number of hosts (5 *P. truei,* 2 *O. leucogaster,* 1 *N. mexicana*) for their cross-infection trials, and consequently, the same hosts had to be reinoculated with the 3 species of *Eimeria* in question. In contrast, all of the *P. maniculatus* and *O. leucogaster* recipients of the present study were previously uninoculated individuals. And, although each of our *N. albigula* had to be reinoculated 3 times, the shortest time period between any subject's reinoculation was 34 days (all others were spaced 5–11 wk apart). In addition, the woodrat that received *E. albigulae* 34 days after being inoculated with *E. arizonensis* supported a patent infection with the former species, and later shed *E. albigulae* oocysts when it was reinoculated with this species 72 days after being given *E. onychomysis.* Similarly, another *N. albigula* was given *E. arizonensis* then, 48 days later, *E. onychomysis*; 55 days after the latter inoculation, the animal was given *E. albigulae* and developed a patent infection. The fact that both woodrats supported patent infections of *E. albigulae* after previously being inoculated with both *E. arizonensis* and *E. onychomysis* should allay the concern that repeated inoculations into *N. albigula* may have affected their immune status and thereby influenced the negative results that we saw in this host species' cross-infection trials (see Upton et al., 1992).

In addition, more than 1 species within *Peromyscus* and *Neotoma* now have been shown to be refractory to cross-infections with the *Eimeria* species in question (Table III). This is important because, as demonstrated by Mayberry et al. (1982), the lack of life-cycle completion of an *Eimeria* in a single strain of animal is not adequate proof that the species cannot serve as a host. Extending the argument of Mayberry et al. (1982), we suggest that the negative results of the cross-infection trials with 2 species of *Peromyscus* and 2 species of *Neotoma* provide additional evidence that *E. albigulae, E. arizonensis,* and *E. onychomysis* are distinct species.

Duszynski (1986) suggested that, when host species are syntopic over extended periods of time, appropriate genetic or ecologic situations may occur that would allow the transfer of a coccidium to a new host and that, once this occurred, selection might operate on these pioneer parasites to produce strains better able to infect other members of the new host species. Therefore, we considered it important to include isolates of coccidia that had been collected from syntopic hosts in the cross-transmission experiments. The isolates of *E. arizonensis* and *E. onychomysis* that we collected from the Sevilleta LTER (Table I) came from animals captured at the same permanent trapping web (Web 1, Creosote—west site; see Wilson et al. [1997] for Global Positioning System coordinates), and the Sevilleta LTER isolate of *E. albigulae* came from a host captured at a site ~600 m from this locality (Web 3, Grassland—west site; see Wilson et al., 1997). All 4 of the cross-infection trials with *E. onychomysis* in the present study, 3 of 4 trials with *E. arizonensis,* and 3 of 4 with *E. albigulae,* were done with these isolates, i.e., with parasites obtained from host species that have been sharing the same environment for hundreds, perhaps thousands, of years. Within the context of Duszynski's (1986) hypothesis outlined above, the failure of these parasites to be cross-transmitted successfully can be considered as additional proof of their host specificity.

Levine and Ivens (1988), in their review of cross-transmission studies with the *Eimeria* of rodents, listed 54 cross-infection attempts between hosts belonging to different genera within the Muridae; these involved 23 *Eimeria* species, 17 host species, and 14 host genera. Of these, 3 attempts were successful, but, as noted by Levine and Ivens (1988), all 3 required special conditions. Todd and Lepp (1972) were able to transmit *Eimeria vermiformis* from *Mus musculus* to *Rattus norvegicus,* but only after treating the latter host with dexamethasone, and Mayberry and Marquardt (1973) and Mayberry et al. (1982) transmitted *Eimeria separata* from *R. norvegicus* to some genetic strains, but not others, of *M. musculus.* Subsequent to the studies reviewed by Levine and Ivens (1988), 5 of 29 attempts to cross-transmit eimerian parasites between different genera of murid rodents were successful (Nowell and Higgs, 1989; Ibrahim and Nowell, 1991; Upton et al., 1992; this study). The 29 attempts involved 8 species of *Eimeria* (6 of which had not been tested

in prior cross-transmission experiments), and 12 species of murids from 8 genera (of which, 8 species and 4 genera were new to experimentation). However, the successful transfer of *Eimeria apionodes* and *Eimeria hungaryensis* from *Apodemus sylvaticus* to *M. musculus* did not occur until the latter host was immunosuppressed with hydrocortisone (Nowell and Higgs, 1989; Ibrahim and Nowell, 1991). Thus, only Upton et al. (1992), who transferred *E. arizonensis* isolated from *Reithrodontomys* to *Peromyscus,* and vice versa, were able to cross-transmit successfully an *Eimeria* species between 2 genera of murid rodents that did not require immunosuppression, or a special genetic background, of the recipient hosts.

Although there is evidence that the *Eimeria* of rodents can be passaged between host species of the same genus (Levine and Ivens, 1988; Upton et al., 1992), exceptions have been reported. Arnastauskiene (1977) was unable to transmit *Eimeria middendorfi* and *Eimeria taimyrica* from *Microtus middendorfi* to *Microtus arvalis*; in addition, he was unable to transmit *Eimeria schiwicki* from *Clethrionomys rutilus* to *Clethrionomys glareolus.* Unfortunately, it cannot be determined if Arnastauskiene (1977) used control animals or replicates in these cross-infection experiments. However, Todd and Hammond (1968a, 1968b) used multiple subjects for their cross-infection trials and determined the viability of eimerian isolates by control infections or in vitro excystation. They found that isolates of *Eimeria lateralis* (which they called *Eimeria larimerensis*; see Seville and Stanton [1993a] for synonymy) obtained from 5 species of *Spermophilus* produced patent infections in 10 cross-species combinations but were not transmissible to *Spermophilus richardsonii* (Todd and Hammond, 1968b). Subsequent to their experimental work, *E. lateralis* was reported from wild *S. richardsonii* (Hilton and Mahrt, 1971; Seville and Stanton, 1993a, 1993b), which suggests that the isolates used by Todd and Hammond (1968b) were idiosyncratic in their inability to produce patent infections in this host species. Similarly, Todd and Hammond (1968a) found that *Eimeria callospermophili* isolated from *Spermophilus beecheyi* did not cause patent infections in *Spermophilus variegatus* (this isolate was transmitted to *Spermophilus armatus* and *S. richardsonii*), but that isolates obtained from *S. armatus, S. richardsonii,* and *S. lateralis* could be passaged through *S. variegatus.*

Thus, there is precedence to our observation that an isolate of *E. langebarteli* recovered from *P. leucopus* could be transmitted to *P. truei* but not *P. maniculatus* subjects (Table II). *Eimeria langebarteli* has been reported from 6 species of *Peromyscus* (Ivens et al., 1959; Reduker et al., 1985; McAllister et al., 1993; Duszynski and McAllister, 1995) and *Reithrodontomys megalotis* (Duszynski et al., 1992) but not from *P. maniculatus.* In the light of the cross-transmission studies (Todd and Hammond, 1968a, 1968b; Mayberry and Marquardt, 1973; Mayberry et al., 1982) and fieldwork (Hilton and Mahrt, 1971; Seville and Stanton, 1993a, 1993b) discussed above, we predict that *E. langebarteli* will be found in wild populations of *P. maniculatus* and suggest that if infection experiments were done with a variety of isolates of *E. langebarteli* and subspecies of *P. maniculatus,* then compatible combinations of these parasites and hosts might be found.

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